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Aquatic Botany 81 (2005) 27–36

Aquatic botany

www.elsevier.com/locate/aquabot

Spatial and temporal variation in RGR and leaf quality of a clonal riparian plant: *Arundo donax*

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Received 11 May 2004; received in revised form 20 October 2004; accepted 2 November 2004

Abstract

Arundo donax L. is a tall perennial reed classified as an emergent aquatic plant. In California, it has invaded riparian zones, where it acts as a transformer species. Because plant growth and leaf quality influence the effectiveness of management techniques, we sought to determine if these characters varied temporally and spatially in a northern California population of *A. donax.* Tissue C and N content and C:N ratio varied during the growing season. Leaf N was higher in spring and in plants that were closer to a stream. It was significantly negatively related to the clump's distance from the stream but not related to its elevation relative to the stream. Plants near the stream produced taller stems with more leaves per stem than those more distant from the stream. RGR differed across time and space. It was highest in spring prior to the appearance of flowers on a few stems that were >1 year old within the clumps. Decline in RGR as the growing season progressed coincided with the appearance of branches and flowers on stems <1 year old on a few plants within the studied population. RGR was significantly related to the N content and C:N ratio of leaves on mature stems (>1 year old). This implies that the decrease in stem growth reflected changes in nutrient availability within the entire *A. donax* clump and not just in the growing stems (<1 year old). These findings have implications for timing of management techniques.
Published by Elsevier B.V.

Keywords: Phenology; Giant reed; Invasive plant; Leaf N content

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0304-3770/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.aquabot.2004.11.001

1. Introduction

Invasive plant species significantly alter ecosystem structure and function (Vitousek, 1990; Vitousek et al., 1997). In riparian habitats throughout the United States, from northern California to Maryland *Arundo donax* is an invasive weed (Bell, 1997), where it often acts as a transformer species (Richardson et al., 2000). For example, a recent report indicated that the total number, total biomass, and taxonomic richness of aerial invertebrates associated with *A. donax* were about one-half of the values associated with native vegetation (Herrara and Dudley, 2003). *A. donax* produces prodigious quantities of biomass (up to 20 t ha^{-1} above-ground dry mass, Perdue, 1958) that is quite flammable at the end of the growing season. As a result, it has changed control of ecosystem processes in some Californian riparian zones from flood-regulated to fire-regulated (Rieger and Kreager, 1989). The removal of this difficult to control species from California riparian zones would improve native species habitat, reduce wildfire threats, and improve water quantity and quality (Bell, 1997).

A. donax is a tall perennial reed that is frequently found growing in water and is thus, classified as an emergent aquatic plant (Cook, 1990). It is a C_3 grass (Rossa et al., 1998) that may grow in large clumps up to several meters across and containing stems (up to several hundreds per clump) that may reach 9 m in height. Although *A. donax* produces flowers, no viable seeds have been detected for plants growing in California (Dudley, 2000). Spring and summer are the main growing seasons for new shoots (Decruyenaere and Holt, 2001; Dudley, 2000).

Little is known about the specific environmental factors that regulate *A. donax* growth or phenological changes that may affect its suitability as a food source for herbivores (Mattson, 1980). How these factors may change spatially within the area occupied by a given population is also not known. Environmental heterogeneity in the availability of resources and population growth or other characteristics is an area of keen interest for ecologists (Bjørnstad et al., 1999; Murrell et al., 2001). Spatial variation in the abundance of plant resources is known to occur. For example, Robertson et al. (1988) measured soil N mineralization at a resolution of 1 m in an old field in Michigan and concluded that heterogeneity at this scale may influence plant population dynamics. In turn, plant spatial pattern strongly affects population dynamics of herbivore species in both natural and agricultural communities. For example, Batch (1984) demonstrated that the distribution of the herbivorous beetle, *Acalymma innubum*, was strongly influenced by characteristics (including leaf quality) of its host plant, a cucurbit vine *Cayaponia americana*, which also varied spatially.

Information on spatial and temporal variation in *A. donax* growth and leaf quality will be important in developing integrated management approaches (Wilen et al., 1996) and may enhance overall understanding of plant phenological patterns (Rathcke and Lacey, 1985). In addition, the growth condition or phenological state of a plant influences its response to management techniques (Ross and Lembi, 1985). Knowledge of how these traits vary spatially may be used to enhance efficacy of existing management practices and to more precisely place these techniques, thus reducing non-target impacts (Rew and Cousens, 2001). The purpose of this study was to determine if growth, plant quality, and nutrient availability varied temporally and spatially in a northern California population of *A. donax*.

2. Methods

2.1. Study area

Most of this work was conducted at the Cache Creek Nature Preserve, Yolo County, California (38°41′18.614″N, 121°52′257″W). The 52-ha preserve had numerous *A. donax* clumps growing within its boundaries. In 1999, we selected 52 *Arundo* clumps and recorded their locations using a Trimble XRS Pro GPS system with real time differential correction. The plants were selected at random but were located in three spatially separated areas of the preserve (Fig. 1). Different numbers of plants were marked in each area. *A. donax* in the West and Center areas were generally nearer the stream. They were also growing amongst a mix of deciduous trees and salt cedar. Those in the East area were generally farther from the stream and the area was more open, less shaded. With the exception of salt cedar plants no other woody species were present in the East area. The greatest distance between two plants within the West area was 247 m. In the Center area it was 161 m, and in the East area it was 154 m. The overall greatest distance between two plants (i.e., the distance between the most westerly plant and the most easterly plant) was 1186 m.

Beginning in January, 1999, we measured the height of 10 stems within a single large *A. donax* clump adjacent to Putah Creek, Yolo County, California (38° 31.423′N, 121°47.090′W).

2.2. Tissue analysis

Starting on April 13, 1999 and at approximately monthly intervals we collected a single leaf from the top of a mature stem (>1 year old) within each clump. Leaf samples were dried at 80 °C for 48 h and analyzed for carbon (C) and nitrogen (N) using a Perkin-Elmer 2400 Series II CHNS/O Analyzer. Acetanilide was used as the standard. Since these data included both fixed (area, date) and random (site) effects, the data were analyzed using a

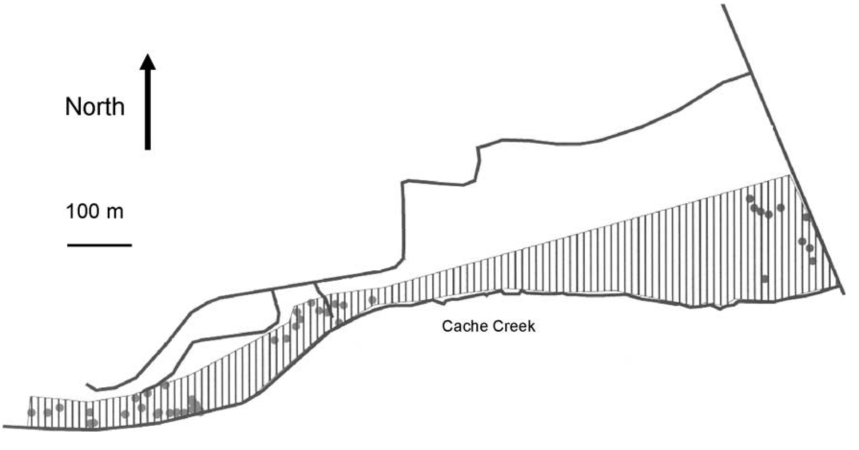

Fig. 1. Location of *Arundo donax* plants (dots) at the Cache Creek Nature Preserve, California. The study area (hatched) was bounded by Cache Creek on the south and by roads within the preserve to the north.

mixed model analysis of variance (PROC MIXED, SAS Institute Inc., 1999; Littell et al., 1996). We used the clump location data set with GPS Pathfinder Office version 2.9 to measure the distance of each clump from the stream. We used a linear regression model (PROC REG, SAS Institute Inc., 1999) to examine the relationship between leaf tissue N and distance from the stream and elevation above the level of the stream.

2.3. Growth rate

Starting April 19, 1999 and at weekly intervals until October 12, 1999 we measured stem height and number of leaves for newly emerged shoots in a subset of the marked clumps. Stem dry weight (g) was estimated from stem height using an equation relating stem height to stem total dry weight for *A. donax* stems less than 1 year old, (stem dry weight (g) = $-5.88882 + 29.85952 \times$ stem height (m), $F_{1,33} = 101.35$, $P < 0.0001$, $R^2 = 0.76$). This equation was estimated from *A. donax* stems collected at a site near Winters, California (Spencer, unpublished data). Relative growth rates (RGR) were calculated by using the logarithm of stem dry weight as the dependent variable in a linear regression versus time (days). Using data prior to June 15 (see below), we examined the relationships between RGR and leaf N and leaf C:N ratio. We also calculated a multiple regression of RGR versus the distance of a clump from the stream and its elevation relative to the stream as described above.

2.4. Soil analysis

On April 27 and October 13, 1999 we collected soil samples from 15 cm deep at the base of each marked clump. These samples were placed in sealed bags, returned to the laboratory and gravimetric water content determined by drying them at 105 °C. On October 13, an additional sample was collected from the base of each clump, air dried, and submitted to the UC DANR Analytical Laboratory for determination of Olsen P (Olsen and Sommers, 1982), total Kejldahl nitrogen (Bremner and Mulvaney, 1982), and soluble K (Thomas, 1982). Organic content was determined as loss on ignition (Brower et al., 1998).

3. Results

3.1. Tissue analysis

Tissue C and N content and C:N ratio varied during the growing season (Fig. 2). Averaged across all sampling areas and sampling dates, tissue C varied less than either tissue N or the C:N ratio (Table 1). Results from analysis of variance indicate that tissue C varied temporally and spatially (Table 2). Leaf N was higher in *A. donax* growing in the West and Center populations which were closer to the stream. Tissue N and C:N ratio also differed across time and sampling area, but the significant statistical interactions indicate that the differences were not always consistent. The nature of the interaction can be seen in Fig. 2. The spatial effect is less obvious at later sampling dates. Using only data from the April sample, we found that leaf tissue N and leaf tissue C:N ratio were significantly negatively related to the clump's distance

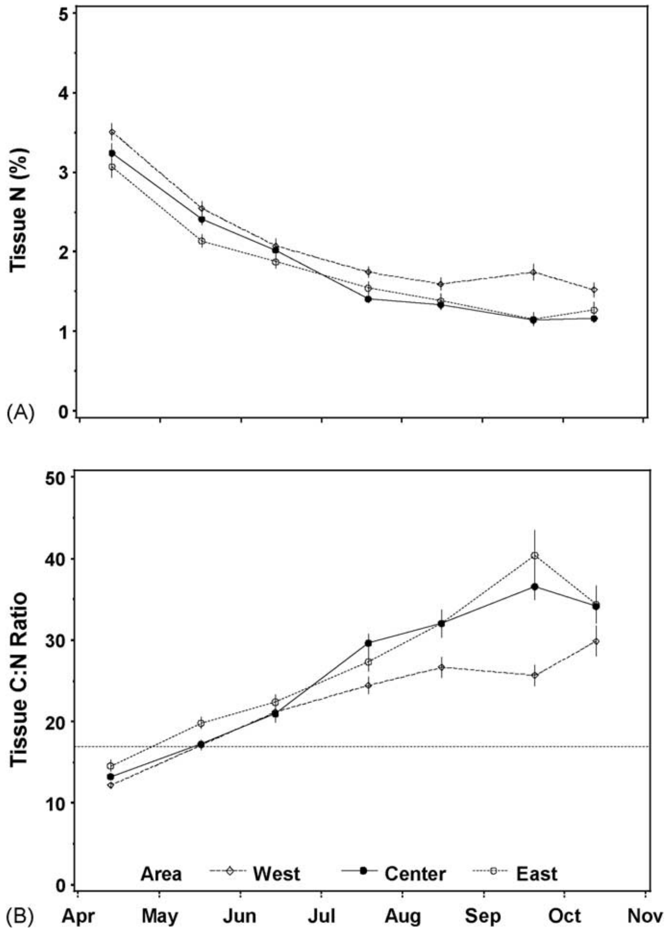

Fig. 2. Leaf tissue N (A) and leaf carbon:nitrogen ratio (B), for *Arundo donax* leaves from stems >1 year old at three sample areas within the Cache Creek Nature Preserve, California. The horizontal line on B represents a C:N ratio of 17. Values are mean ± 1 S.E.

from the stream (N (%) = 3.49 + 0.05 × elevation (m) − 0.005^A × distance (m), $P = 0.06$, $R^2 = 0.13$, superscript *A* indicates the partial regression coefficient was significantly different from zero) but not related to the clump's elevation above the stream (C:N = 12.26 − 0.16 × elevation (m) + 0.02^A × distance (m), $P = 0.02$, $R^2 = 0.13$).

Table 1
Summary statistics for *Arundo donax* leaf tissue nutrient concentrations and ratios at Cache Creek Nature Preserve, California, based on samples collected across time and space

Variable	Mean	S.E.	Coefficient of variation	*N*
C	40.51	0.13	8.2	612
N	1.96	0.03	43.6	612
C:N	24.5	0.41	41.6	612

Table 2
Results of mixed model analysis of variance testing for the effects of sampling date (Date) and sampling area (Area) on *Arundo donax* leaf tissue nutrient concentrations and ratios and relative growth rate (RGR) (results are from type 3 tests)

Variable	Effect	Numerator DF	Denominator DF	*F*-value	*P*
Leaf C	Area	2	26.3	3.43	0.05
	Date	6	551	8.58	<0.0001
	Area × Date	12	551	1.50	0.16
Leaf N	Area	2	25	4.53	0.02
	Date	6	549	275.86	<0.0001
	Area × Date	12	549	2.19	0.04
Leaf C:N	Area	2	27.5	5.02	0.01
	Date	6	550	154.06	<0.0001
	Area × Date	12	550	6.27	<0.0001
RGR	Area	2	43.3	10.76	0.0002
	Date	17	328	11.06	<0.0001
	Area × Date	34	328	1.58	0.0238

3.2. Plant growth

A. donax in the West sample area produced taller stems with more leaves per stem, plants from the East sample area were the shortest and had the fewest leaves per stem, while those in the Center area were intermediate (Table 3). RGR differed across time and space, but the significant statistical interactions indicate that the differences were not always consistent (Table 2). The nature of the interaction can be seen in Fig. 3. Differences in RGR were more profound in spring prior to the appearance of flowers on stems that were >1 year old. Following the second week in June, RGR declined as the growing season progressed (Fig. 3). Reduced stem growth coincided with the appearance of branches and flowers on stems <1 year old. A similar seasonal growth pattern was observed for stems in the single clump at Putah Creek. Because these measurements started earlier in the year, the period of peak RGR values was more clearly delineated (data not shown).

For the Cache Creek *A. donax*, RGR for stems (<1 year old) was positively related to tissue N for leaves on stems in the same clump that were >1 year old (RGR = $-0.03790 + 0.03249 \times$ leaf tissue N (%), $P < 0.0001$, $R^2 = 0.30$). It was negatively related

Table 3
Mean stem height and number of leaves per stem at the end of their first growing season for newly emerged *Arundo donax* stems at three sample areas within the Cache Creek Nature Preserve, California (*N* is the number of stems measured and S.E. is the standard error)

Area	Stem height (m)	S.E.	Lower 95% C.I.	Upper 95% C.I.	Number of leaves per stem	S.E.	Lower 95% C.I.	Upper 95% C.I.	*N*
West	5.49	0.27	4.92	6.05	29.4	1.4	26.6	32.3	21
Center	5.03	0.42	4.06	5.99	27.0	1.2	24.2	29.8	9
East	3.66	0.19	3.27	4.06	24.7	1.2	22.1	27.2	18

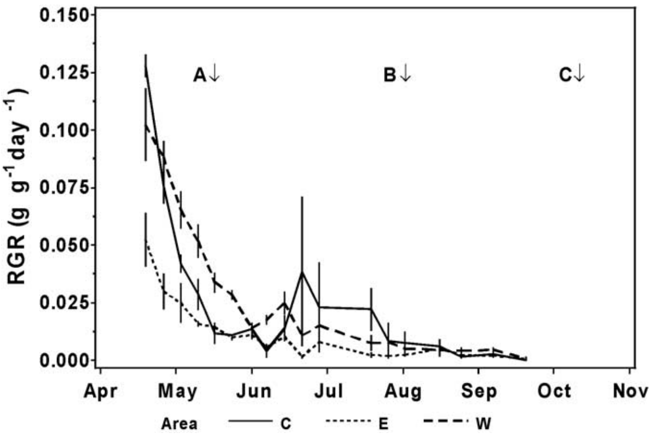

Fig. 3. Relative growth rates (RGR) for newly emerged *Arundo donax* stems during their first growing season at three sample areas within the Cache Creek Nature Preserve, California. The arrows indicate (A) first appearance of flowers on stems >1 year old, (B) first appearance of branches on stems <1 year old, and (C) first appearance of flowers on stems <1 year old.

to tissue C:N ratio for these leaves ($RGR = 0.10398 - 0.00340 \times$ leaf tissue C:N, $P < 0.0001$, $R^2 = 0.28$). Thus, it may be possible to estimate the period of most rapid growth by measuring changes in leaf tissue N content or the leaf tissue C:N ratio. The fact that RGR was related to changes in N content and C:N ratio of leaves on mature stems (>1 year old) suggest that the decrease in stem growth reflects changes in nutrient availability within the entire *A. donax* clump and not just in the growing stems (<1 year old).

3.3. Soil analysis

Mean gravimetric soil water content at the base of *A. donax* clumps was higher in spring than at the end of the growing season in October (Table 4). Soil water content decreased depending on plant location. The decrease ranged from 37% to 58% of initial values. Plants in the West and Center areas were closer to Cache Creek. These plants were likely able to

Table 4
Selected soil properties (total Kejldahl N (TKN), soluble K (sol K), and Olsen P) in three areas of the Cache Creek Nature Preserve, California on 10/13/99

Area	TKN		Sol K		Olsen P		OM		Moisture (%)		Reduction (%)
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	4/23	10/13	
West	437	46	48.8	2.4	13.6	21.8	8.4	1.3	17.8	8.4	53
Center	550	46	23.1	2.1	1.6	25.1	6.4	0.6	10.7	6.7	37
East	805	71	31.0	5.3	6.7	31.8	6.7	0.6	15.3	6.3	58

Values are the mean and standard error (S.E.) and are in mg kg^{-1}, except organic matter (OM) which is in (%). There were 22, 12, and 10 samples in the West, Center, and East areas, respectively, except for organic content when there were 19, 12, and 12 samples, respectively. The column labeled moisture (%) gives the mean soil moisture (gravimetric) on two dates in 1999. Reduction (%) shows the percent decrease in soil moisture between these dates.

access the shallower water table in these areas. (Sher and Spencer, unpublished data indicate that *Arundo* roots quickly grow to >1 m depth). It also possible that soils in these areas had higher moisture content because of shallowness of the water table here. Thus, moisture levels were replenished more readily. Plants in the East sampling area were more distant from Cache Creek. Thus, the soil water content in this area likely reflects conditions that may limit growth.

Differences in soil nutrient levels at the three areas within the nature preserve may also have influenced *A. donax* growth rates (Table 4). At the end of the growing season, available P and Kejldahl N were lowest in the areas, which supported the highest growth and had higher leaf tissue N levels in spring. Soluble K levels were also highest in areas, where growth was greatest. This may be in part be due to the fact that K sufficient plants are more resistant to drought stress than K deficient plants (Marschner, 2002). Higher levels of K and N being associated with higher RGR is also consistent with information indicating that full utilization of soil N by crop plants only occurs when the soil K supply is adequate (Mengel and Kirby, 1982) Thus, the pattern of soluble K and Kejldahl N is consistent with the observed higher tissue N levels in areas with higher growth rates. Organic matter content did not differ greatly among the three areas.

4. Discussion

Leaf N is important in plant herbivore interactions (Newman et al., 1998; Mattson, 1980). Thus *A. donax* in the West and Center populations may be more suitable food items. Leaf C:N ratio is another indicator of food quality. *A. donax* leaf C:N ratio was generally >17 after mid-May and thus, *A. donax* leaf tissue was outside the range of C:N ratios ($\leq$17) believed to be favorable to aquatic herbivores (Russell-Hunter, 1970; McMahon et al., 1974). These data indicate that leaf N content would be more favorable to herbivores early in the growing season and for plants closer to the stream.

A. donax RGR were similar to values reported for other grass species. Ryser and Wahl (2001) reported that RGR for 24 grass species in 13 genera varied from 0.034 to 0.214 g g^{-1} day^{-1}. Villar et al. (1998) reported that RGR for 20 grass species in the genus *Aegilops* varied from 0.116 to 0.187 g g^{-1} day^{-1}. Reich et al. (2003) reported that RGR for seven species of C_3 grasses ranged from 0.08 to 0.151 g g^{-1} day^{-1}. Seventy-five percent of the RGR values for *A. donax* at Cache Creek were between 0.003 and 0.189 g g^{-1} day^{-1}. *A. donax*'s apparent larger range of RGR values than these other grasses is probably due to variation in growing conditions over the course of the season at Cache Creek, which was likely greater than the variation in growing conditions used in the cited reports. Interestingly, *A. donax* RGR values early in the growing season were greater than values reported by Reich et al. (2003) for two species of oaks (0.022–0.031 g g^{-1} day^{-1}).

These findings also have implications for *A. donax* management techniques. Ross and Lembi (1985) indicate that the time to begin control practices for perennial weeds is related to the development of the plant over the season. Plants are most susceptible to control efforts during periods of rapid growth or when carbohydrates are moving downward towards underground storage organs. The seasonal patterns of shoot elongation, leaf production, and RGR observed for *Arundo* indicate that growth was most rapid prior to the second week in June. These data also indicate that the period of rapid growth was not the same at the three sites examined. Thus, to be most effective at sites similar to those studied, treatments might be applied earlier in the growing season for *Arundo* located farther from the stream edge or in drier or otherwise less hospitable habitats. Also, Rew and Cousens (2001) indicate that using spatial differences in growth within a population to enhance efficacy of management techniques will result in more precise management, reducing exposure and impacts for non-target species.

Acknowledgments

Dr. John Madsen and Dr. David Thornby read an earlier version of the manuscript and provided helpful comments. Mention of a manufacturer or product neither constitute a warranty or guarantee of the product by the U.S. Department of Agriculture nor an endorsement over other products not mentioned.

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